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PIMPINELLA SAXIFRAGA IS MAINTAINED IN ROAD VERGES BY MOSAIC MANAGEMENT

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Abstract

Road verges have been proposed as refuges for vulnerable grassland species in the modern, changing landscape, but little comparative knowledge exists on how management regimes affect population dynamics of such species. We compared the effects of various management regimes on population dynamics of *Pimpinella saxifraga* in road verges and pastures, using elasticities and LTRE-analyses with underlying vital rates as model components in three road verges and three pastures in a agricultural landscape in western Norway. Under present management regimes, we observed slightly higher projected population growth rates in pastures than in road verges. The pasture populations had comparatively lower survival but higher reproduction than the road verge populations, thus demonstrating a management-induced negative correlation. Such negative correlations generally increase species' adaptability to environment changes, thereby reducing the extinction risk. We generally observed small changes in *P. saxifraga* demography to management but considerable variation along environmental gradients, underlining the importance of studying multiple populations. The linear form of the road verges enabled a fine-scale mosaic application of different management regimes. Individuals growing in zones receiving survival-lowering management produced seeds that compensated the lack of seeds in zones receiving fertility-lowering management. The study indicates that road verges may represent refuges for vulnerable grassland species like *P. saxifraga*, given proper management. The observation of 'mosaic' management that allows road verge metapopulations to complement each others life-history characteristics exemplifies the unique potential of road verge ecosystems to maintain semi-natural grassland species, as well as providing habitats for different species exhibiting various life histories.

Key-words: LTRE, mosaic management, population growth rate, resource allocation trade-offs, semi-natural grassland, source-sink populations, vital rates

1. Introduction

Semi-natural grasslands such as pastures and meadows represent highly valuable elements of the European cultural landscape (Kull and Zobel 1991; Norderhaug et al. 2000). However past land-use changes have led to major losses of species-rich, specialized grasslands (Lennartsson and Oostermeijer 2001; Pykälä 2000) where road

verges often provide refuge for native species, existing in alternative grassland 'states' (Cousins 2006; Forman and Alexander 1998; Koyanagi et al. 2009). Road verge management (e.g. mowing, which is carried out for traffic safety reasons) can often generate suitable habitats for grassland species and other species (Auestad et al. 2008; Cousins and Eriksson 2002; Spooner et al. 2004) and maintain populations, depending on the intensity, frequency and nature of the disturbance event (Spooner 2005). So far, the main focus of road verge management evaluations has been on species composition and diversity (e.g. Jantunen et al. 2006; Parr and Way 1988; Schaffers 2002; Tikka et al. 2000), rather than on plant populations (but see Endels et al. 2007; Jantunen et al. 2007). By comparing population dynamics of target species in road verges and traditional grasslands, we can identify the extent to which road verges act as refuges (Brys et al. 2004; Lennartsson and Oostermeijer 2001).

Among species adapted to the light-open, infertile conditions of semi-natural grasslands is *Pimpinella saxifraga*, a low-growing umbellifer considered an indicator species of old grasslands (Grime et al. 2007). Such species are suppressed in derelict or fertilised grasslands, and therefore declines in the modern landscape due to land-use changes. Demographic studies of how species like *P. saxifraga* behaves in continuously managed grasslands (meadows and pastures) as compared to 'novel' grasslands such as road verges may elucidate the importance of road verges as refuges for species from meadows and pastures. Comparisons of management regimes in road verges and traditional grasslands, respectively, may guide the choice of appropriate management regimes for maintaining declining semi-natural grassland species.

Matrix transition models provide powerful tools for studying the demography and population dynamics of populations (Caswell 2001), often employing matrix elements as basic model components. However, each matrix element is a function of more than one underlying (lower-level) *vital rate* (survival, growth and reproduction, Caswell 2001). The relative importance (elasticity) of a vital rate to the population growth rate (λ) reveals how hypothetical changes in that vital rate would alter λ (de Kroon et al. 2000). Life-table response experiments (LTRE) moreover decompose observed differences in λ into the contributions from individual demographic variables (Caswell 2001). A LTRE based on vital rates may pinpoint the effect of management regimes on specific vital rates, thereby permitting more efficiently directed management decisions.

In this study, we evaluate the effect of the present management regimes in road verges and pastures on *P. saxifraga*, using underlying vital rates as model components. We also assess the impact on the vital rates of three alternative (i.e. with different mowing and hay removal) road verge management regimes, and the impact of one alternative (i.e. traditional) pasture management regime. We compare population growth rates (λ) in different sites and under different treatments, and relate them to elasticity patterns of underlying vital rates. The vital rates responsible for differences in λ between treatments are identified by LTRE analyses.

2. Material and methods

2.1 The species

Pimpinella saxifraga is a low-growing, perennial umbellifer growing on short turf (Grime et al. 2007). Seedlings and young plants possess small, circular leaves. When the plant matures, a prostrate, basal rosette of pinnate leaves that may stay green through winter substitute the circular leaves. *P. saxifraga* produce an apical inflorescence in July with white flowers in compound umbels, and shed seeds in late

summer/early autumn. The plant has limited ability for clonal growth, but side-rosettes may be formed on short extensions of the main tap-root, and usually stay connected to the mother plant. The tap root provides access to moisture in soil crevices, thus enabling the plant to survive under dry conditions. It mainly grows in infertile, calcareous, human-influenced habitats, e.g. pastures and meadows, road verges and ridges. The species occurs in lowland areas in most of Europe except the extreme south (Grime et al. 2007) and is fairly common in Southern Norway (Lid and Lid 2005). However, due to its low-growing stature it is easily overgrown in derelict or fertilised grassland and consequently, *P. saxifraga* is believed to be currently decreasing (Grime et al. 2007).

2.2 The study system

We performed the study in Lærdal, Sogn og Fjordane county, W Norway (61°04'N, 7°32'–49'E) in three pastures and three road verges holding large populations of *P. saxifraga*. The sites were situated within 11 km distance, at altitudes from 35 to 420 m a.s.l., all faced south (from SE to SW). Areas of the pastures varied from 2.8 to 7.5 ha while the road verges comprised narrow (3–5 m) strips of 50–100 m lengths alongside roads. All study sites were situated on terraces formed by eroded glacifluvial deposits (Klakegg et al. 1989). The bedrock consisted of Precambrian gneisses, except for one site on gabbro (Klakegg et al. 1989). All sites were situated in the southern boreal, slightly continental region (Moen 1999), had low annual precipitation (ca. 500 mm, Førland 1993) and annual mean temperature of ca. 5.9 °C (Aune 1993) for the period 1961–1990.

The three pasture sites [Molde pasture (MP), Stuvane pasture (SP) and Nese pasture (NP)] had received traditional grassland management for centuries: spring and autumn grazing (generally by sheep from late May to Mid June and from late August till late September, respectively), and no fertilization. MP and NP had also traditionally been mown in July, but cutting had ceased completely or been carried out only infrequently over the last 20 years.

Two of the road-verge sites, Molde road verge (MR) and Stuvane road verge (SR), lay close to the MP and SP sites, respectively, and had a common management history before road improvement (ca. 1950). The Nese road verge (NR) was established during widening of the road in 1964 and had no former history of grazing or cutting. This verge lay ca 1 km from NP and bordered abandoned grassland dominated by young *Alnus incana*. Since 1990, the road verges have been annually managed by a mid-June cutting (hay left at site) of the zone closest to the road bed (1–2 m breadth), and a second cut in August, covering 3 m breadth from the road bed and inwards. In wider road verges (> 3 m breadth) the innermost parts are never cut.

2.3 Experimental setup

In each of the six study sites we placed six blocks of 15 – 16 m² and lay out permanent quadrats of 0.5 × 0.5 m with buffer zones of 0.25 m at all sides at random within each block, four in each road verge block and two in each pasture block. Quadrats with buffer zones were not allowed to share sides, thus ensuring minimum between-quadrat distances of 0.7 m (for further details see Auestad et al. 2008).

We mapped and tagged *P. saxifraga*-individuals (ramets) in the 108 quadrats and censused their survival, growth and flowering in August 2003 – 2006. Altogether we monitored 2301 individuals for one or more transitions, summing up to 4583 observations. Six quadrats experienced misplaced management by the Road Authorities in 2005. We discarded two of these and substituted the other four by four new, closely

positioned quadrats. In some quadrats, we restricted censuses to a subpart due to extremely high seedling density.

2.4 Treatments

In the road verges, we applied four different management treatments, replicated within each block: V1 comprised early (June) and late (August) cut with no removal of hay, thus mimicking the outer road verge management regime. V2 also comprised early and late cutting, but with hay removal. In V3, we cut and removed hay in August only. Finally, we applied a treatment with no active management (V4). We also investigated two management regimes for the pastures, replicated within each block. P1 represented the present treatment (spring and autumn sheep grazing) and P2 the traditional management regime (spring and autumn sheep grazing, late cut and removal of hay). We cut the grass annually 5 – 10 cm above the ground in week 25 – 26 (early cutting) and week 33 – 34 (late cutting, after census) in all four years of the study. We applied the treatments to quadrats and buffer zones, but censused only plants growing in the 0.5 x 0.5 m quadrat. During the study period, site NP had high stocking rates in both spring and autumn, site MP experienced varying grazing pressure in spring and thorough grazing in autumn, whereas site SP generally had low stocking rates.

2.5 Stage and size classes

We combined plant size (dry mass (g), DM) and stage (flowering or non-flowering) to classify the *P. saxifraga* individuals into five classes. These characteristics related significantly (judged by GLM regression analyses) to the demographic fate of the individuals. We estimated the DM and the potential seedling production of each individual from in situ morphological measurements of characters by GLM regression (see Appendix A in Supporting Information). The five classes are:

(1) Sdl (Seedlings): circular leaves, DM less than 0.031 g. The term ‘seedling’ is used in a broad sense, also including tiny plants germinated in previous years with high mortality (40%) and zero probability of flowering the following year.

(2) SNF (Small non-flowering individuals): pinnate leaves, DM between $9.8 \cdot 10^{-4}$ g and 0.031 g, lower mortality than Sdl (22%) and low flowering probability at time $t+1$ (8%). The pinnate leaves indicated a higher maturity level than Sdl. We therefore chose to separate these classes despite overlapping size categories.

(3) LNF (Large non-flowering individuals): pinnate leaves, DM between 0.031 g and 1.000 g and 28% probability of flowering at time $t+1$.

(4) SF (Small flowering individuals): DM between 0.022 g and 0.25 g, average seedling production of 0.97 per individual at time $t+1$ and 43% probability of flowering at time $t+1$.

(5) LF (Large flowering individuals): DM between 0.25 g and 22.6 g, average seedling production of 1.73 per individual at time $t+1$ and 44% probability of flowering at time $t+1$.

We omitted a seed stage as *P. saxifraga* has a predominantly transient seed bank (Grime et al. 2007). We observed few cases of clonal growth ($n = 62$) and dormancy ($n = 39$). A separate elasticity analysis of an eight-stage model including two clonal (non-flowering and flowering) and one dormant class revealed minor impact on λ (elasticity values of 1%, 1% and 5%, respectively, results not shown) and we therefore left these classes out of the model. We treated clonal offspring as any other individual in the analyses. The transitions of the dormant individuals were incorporated in the matrix as a form of stasis.

2.6 Matrix parameterisation

We constructed projection matrices for the eighteen site-treatment combinations and for the overall, pooled population, in which each element (a_{ij}) represented the transition from the j^{th} category in year t to the i^{th} category in year $t+1$ (Caswell 2001). To obtain sufficiently large data sets for calculation of transition probabilities for all combinations we pooled data from the three transition periods. The number of observed individuals in class SF (small flowering individuals) in the NV3 population was deemed insufficient ($n < 5$) and for this class we based the calculations of transition probabilities to all other classes on aggregate data for SF of the overall populations (cf. Menges and Dolan 1998). Each matrix entry is a function of a combination of the following lower-level vital rates (Franco and Silvertown 2004; Jongejans et al. 2006): survival (σ_j), growth (conditional to survival; $\gamma_{i>j}$), stasis (conditional to survival; $\gamma_{i=j}$), retrogression (conditional to survival; $\gamma_{i<j}$), seed production (ε_j) and site-specific seedling establishment probability (ω).

σ_j (survival) is the probability that a plant individual survived until time $t+1$, and γ_{ij} (growth) the probability that a surviving individual in class j grew into size class i . Progressive growth ($\gamma_{i>j}$) implied that the individual increased in size or went from non-flowering to flowering individual, retrogressive growth ($\gamma_{i<j}$) that the individual decreased in size or changed into non-flowering, and stasis growth ($\gamma_{i=j}$) that the individual stayed in the same size class.

The fertility transitions (a_{14} and a_{15}) consisted of ω , the site-specific establishment probability per seed and ε_j , the average number of seeds produced per individual in class j . ω was quantified by relating the seedlings emerging at time $t+1$ to the number of seeds produced at time t per area unit in demographic quadrats of each of the six sites (see Appendix B for a full explanation of ω calculations) as described in Eqn. 1:

$$\begin{bmatrix} \sigma_1\gamma_{11} & 0 & 0 & \varepsilon_4\omega & \varepsilon_5\omega \\ \sigma_1\gamma_{21} & \sigma_2\gamma_{22} & \sigma_3\gamma_{23} & \sigma_4\gamma_{24} & \sigma_5\gamma_{25} \\ \sigma_1\gamma_{31} & \sigma_2\gamma_{32} & \sigma_3\gamma_{33} & \sigma_4\gamma_{34} & \sigma_5\gamma_{35} \\ 0 & \sigma_2\gamma_{42} & \sigma_3\gamma_{43} & \sigma_4\gamma_{44} & \sigma_5\gamma_{45} \\ 0 & \sigma_2\gamma_{52} & \sigma_3\gamma_{53} & \sigma_4\gamma_{54} & \sigma_5\gamma_{55} \end{bmatrix} \quad \text{Eqn. 1}$$

The vital rates values for the 18 site-treatment matrices and the overall matrix are given in Appendix C.

2.7 Matrix analyses

For each of the 18 population transition matrices and the overall matrix we calculated the projected population growth rate (λ) and estimated the means and 95% confidence intervals by bootstrapping (Caswell 2001; Kalisz and McPeck 1992), re-sampling ‘individuals’ 1000 times by bootstrapping from the different data sets. The overall matrix was bootstrapped using the fixed value of mean ω multiplied by the mean ε_j of all the 18 habitat-treatment populations as estimates of the matrix elements a_{14} and a_{15} . To obtain reliable estimates of the vital rates for the small NV3 population ($n < 5$), we used the site-specific value of ω multiplied by the mean ε_j of all the 18 habitat-treatment populations as estimates of a_{14} and a_{15} .

We calculated elasticities for vital rates by tracking the proportional changes in λ resulting from proportional changes in the vital rates x_k implicit in matrix elements a_{ij} . By rescaling the absolute values of all e_{xk} in each matrix to sum to one, we enabled comparisons of e_{xk} between different populations (sensu Franco and Silvertown 2004).

We performed two-ways LTRE's (fixed effects; Caswell 2001 p. 275) by using the vital rates as model components to decompose the variation in λ in contributions of habitat or treatment effects (α), site effects (β) and their interactions ($\alpha\beta$). To quantify the contribution of a given vital rate x_k , the differences of between x_k of the matrix of interest, and the corresponding x_k of the reference matrix, $A^{(ref)}$ were multiplied with the sensitivity value of the same vital rate computed from the matrix halfway between the matrix of interest and $A^{(ref)}$ (Caswell 2001 p. 275; Zuidema et al. 2007). The LTRE model with two factors (Caswell 2001; Jongejans and de Kroon 2005) is given by:

$$\lambda^{(mn)} \cong \lambda^{(ref)} + \alpha^{(m)} + \beta^{(n)} + (\alpha\beta)^{(mn)} \quad \text{Eqn. 4}$$

in which a given λ of treatment m and site n is written as the sum of the dominant eigenvalue of the reference matrix $\lambda^{(ref)}$, the main effect of habitat or treatment m , $\alpha^{(m)}$, the main effect of site n , $\beta^{(n)}$, and the residual 'interaction effect' $\alpha\beta^{(mn)}$, (Horvitz et al. 1997). The LTRE effects can be decomposed into positive or negative contributions from the different matrix elements.

In particular, we performed three separate LTRE's (similar to Planned Comparisons in ANOVA). (1) Present road verge treatment V1 vs. present pasture treatment P1, using the average matrix of the six treatment-site matrices (treatments V1 and P1 in the three sites M, S and N) as reference matrix. (2) Present (V1) vs. alternative road verge treatments (V2-V4), using the average matrix of V1 as reference matrix (V1 averaged over all three sites M, S and N). (3) Current (P1) vs. traditional pasture treatment (P2) using the average matrix of P1 (averaged over all three sites M, S and N) as a reference matrix. For each of the three comparisons, we also compared the three sites (averaged over the treatments in question) to the relevant average matrix (see Appendix D for the vital rates for all averaged matrices).

3. Results

3.1 Transition probabilities

Pimpinella saxifraga had high survival ($\sigma_j \geq 0.78$) in all but the seedling (Sdl) stage ($\sigma_1 = 0.60$; Fig 1, Appendix C). Seedlings (Sdl) tended to grow to small non-flowering (SNF) and large non-flowering (LNF) stage and stay in these classes ($\gamma_{22} = 0.57$ and $\gamma_{33} = 0.55$). Few LNF plants matured into flowering classes, whereas small (SF) and large flowering (LF) individuals commonly became LNF after flowering (Fig 1). Seed production was much higher in LF than in SF ($\varepsilon_5 = 108.64$ and $\varepsilon_4 = 36.72$). The low site-specific seedling germination rate ($\omega = 0.0103$ averaged over sites) greatly reduced seedling numbers.

3.2 Population growth rates

P. saxifraga had overall population growth rate (λ) of 0.947 (Fig. 2, upper panel). Road verges receiving present treatment (V1; early and late cut and no removal of hay) all had λ 's < 1 , and differed little from treatment V2 (early and late cut with removal of hay). Two out of three populations receiving treatment V3 (late cut and removal of hay) had significantly higher λ 's than V1 and V2. Populations receiving no management (V4) got slightly (but not significantly) higher λ 's than the V1 populations.

The pasture populations included both the highest (1.236 for MP2) and the lowest (0.672 for SP1) λ values (Fig. 2a) but in general, λ differed far more between sites than between treatments.

3.3 Elasticity patterns

Survival probabilities (σ_j) generally had high λ elasticity values, while vital rates related to fertility (ε_j and ω) contributed less to λ (Fig. 2. lower panel). λ values correlated significantly negatively to the elasticities of σ_j (Kendall non-parametric rank test, $\tau = -$

0.59, $P = 0.0011$, $n = 18$) and retrogression ($\tau = -0.60$, $P = 0.0006$, $n = 18$) and significantly positively to the elasticities of ε_j and ω ($\tau = 0.58$, $P = 0.0012$, $n = 18$).

The elasticity values of the present road verge (V1) and pasture (P1) treatments (Appendix E, Table E1) showed that growth rates ($\gamma_{i>j}$) impacted λ more in pastures (21%) than in road verges (13%) whereas retrogression and stasis ($\gamma_{i>j}$ and $\gamma_{i=j}$) cumulatively showed an opposite pattern (23% and 37%, respectively). Sexual reproduction (ε_j and ω) contributed ca 10% in pastures but gave by definition zero contribution in road verges under present management regime (V1), because the repeated cuttings of V1 prevented normal seed production.

Comparisons of all road verge treatments (Fig. 2b) showed only slight differences in elasticity of λ to growth. Stasis and retrogression had equal effect on λ in V1 and V2, whereas in V3 and V4 stasis contributed relatively more and retrogression relatively less to λ . Comparisons of the two pasture treatments (P1 and P2) revealed less variation between treatments than between sites.

3.4 LTRE analyses: treatment effects

All LTRE analyses fitted well, as observed and computed differences in λ had average deviation of 0.31% and maximum variation of 1.15% (see Appendix E for contributions from the vital rates).

P. saxifraga performed slightly better in presently treated pastures (P1; $\lambda = 0.940$) than in presently treated road verges (V1; $\lambda = 0.879$) when compared to the average matrix ($\lambda = 0.908$). V1 gave lower fertility than P1 as the two annual cuttings prohibited seedling production (ε_j) whereas P1 allowed normal seedling production. Lower survival and stasis reduced λ in pastures relative to road verges (Fig. 3a). However, λ varied more between the three sites than between the two treatments (Fig. 3a, b). The low λ of site Stuvane compared to site Nese (0.671 and 1.040, respectively) reflected low survival and fertility (Fig. 3b) and increased growth into the largest size classes in site Stuvane reduced these differences in λ only slightly.

Comparisons of the three alternative road verge treatments (V2–4) using the averaged V1 matrix as reference ($\lambda = 0.879$) showed that *P. saxifraga* performed slightly better under all alternative treatments than the present treatment (Fig. 4). V2 differed little from V1 ($\alpha = 0.024$), probably because both treatments included two cuttings (Fig. 4a). Reduced cutting frequency under V3 and V4 allowed normal seedling production, and the higher ε_j increased λ (Fig. 4a). As the establishment probabilities (ω) were site-specific, but not treatment-specific, they gave no contribution to differences in λ . Lower survival of seedlings and flowering individuals reduced λ for V3 and V4. In V4, high stasis increased λ but lower growth and retrogression ($\gamma_{i<j}$ and $\gamma_{i>j}$) counteracted the effect, giving a moderately positive effect ($\alpha = 0.067$).

We found a slight increase in λ ($\alpha = 0.036$) under traditional pasture treatment (P2) when compared to P1 averaged over sites ($\lambda = 0.940$, Fig. 5a). Under P2, λ increased in response to higher σ_j . As for the road verge treatments, ω were identical for P1 and P2. In contrast to the moderate overall treatment-effect, P2 affected *P. saxifraga* differently in the three sites ($|\alpha\beta| = 0.182$) (Fig. 5b). λ increased in site Molde ($\beta = 0.299$), decreased in site Stuvane ($\beta = -0.209$) but changed little in site Nese ($\beta = -0.002$). In Molde, high σ_j and growth ($\gamma_{i<j}$) and ω of 0.022 increased λ considerably (Fig. 5b, Appendix E, Table E3). In site Stuvane, lower σ_j reduced λ , while low seedling establishment ($\omega = 0.001$) caused the largest single negative contributions (Fig. 5b, Appendix E, Table E3). In site Nese, weaker growth of LNF individuals into flowering

stages decreased λ greatly (Fig. 5b, Appendix E, Table E3), but higher survival and stasis rate of LNF individuals buffered the overall effect on λ .

4. Discussion

Our study demonstrates population growth rates slightly below unity in most of the 18 site-treatment populations of *Pimpinella saxifraga*. The comparison of the present management regimes of pastures (spring and autumn grazing, P1) and road verges (two annual cuttings and no hay removal, V1) indicates that present pasture management provides moderately better conditions than present road verge management, as do the three alternative road verge regimes examined in this study (V2–V4). Traditional pasture management which include annual cutting in addition to grazing (P2) yields slightly higher λ than present management (spring and autumn grazing only; P1).

The use of vital rates instead of matrix elements as model components enabled us to differentiate between effects of survival (σ_j), different aspects of growth (γ_{ij}) and fertility (ω and ε_j) on λ . When estimating seedling establishment probability (ω) we assumed no differences between treatments within habitats (pastures and road verges). However, the treatments obviously differed, for instance regarding litter accumulation which is known to generally reduce seedling establishment probability by reducing quantity and quality of light (Facelli and Pickett 1991). However, since *P. saxifraga* seedling emergence is little reduced by litter (Hovstad and Ohlson 2008) we argue that the parameterization of the seedling germination rate ω used in our model is realistic.

The elasticity analysis of the 18 treatment-site populations confirmed the recognized pattern of populations with low λ relying more on survival and populations with high λ relying more on fertility (Menges and Dolan 1998; Oostermeijer et al. 1996; Valverde and Silvertown 1998). The tap-root of *P. saxifraga* probably contributed to the species' high survival rates as such perennial structures generally ensure low mortality (Ehrlén 2000). However, as reproduction rates may vary much more than survival rates; the theoretically most elastic vital rates (survival) may be much less susceptible to changes in the environment than the less elastic rates of reproduction (de Kroon et al. 2000).

4.1 Road verges maintain the traditional grassland species *P. saxifraga*

The LTRE-analysis indicated that under present management regimes (P1 and V1), pastures represented better habitats for *P. saxifraga* than road verges as the latter prohibited normal seedling production. A general increase in survival in all classes but seedlings and small non flowering plants under road verge cutting without hay removal (V1) partly countered the low fertility. An opposite survival pattern was found for the early-flowering *Primula vulgaris* that experienced significantly increased seedling and juvenile survival due to cutting (Endels et al. 2007). *P. vulgaris* is sensitive to litter accumulation for seedling establishment (Valverde and Silvertown 1995) and cutting probably improved seedling and juvenile survival. The increased survival of flowering plants under present road verge treatment (V1) exemplified a negative correlation between fecundity and longevity, possibly through resource allocation trade-offs as found for *P. saxifraga* by Huhta et al. (2009) as well as for other perennial species (Brody et al. 2007; e.g. Obeso 2002). Cutting the inflorescences probably improved survival through increased resource allocation into the rosette-leaves, paralleling the increase in total weight and side rosettes production in *Hypochaeris radicata* after flower bud removal (Hartemink et al. 2004). Countering of negative LTRE contributions by positive contributions has been described as more or less a general

pattern (Jongejans et al. 2008), and such buffering of variation to λ generally reduces the extinction risk of species (Morris et al. 2008).

4.2 Alternatives to the present road verge management regimes

The comparison of the four road verge management regimes showed that both treatments including two cuttings, either without (V1) or with removal of hay (V2) lowered λ significantly under unity. The single cutting with hay removal (V3), on the other hand, allowed seedling production and hence increased λ . Also no active management (V4) allowed seedling production, but resulted in tall vegetation that shaded out smaller plants, thus lowering their survival. Lack of management may over time induce overgrowth and a shift towards senescent population structure (Endels et al. 2007; Oostermeijer et al. 1996). However, no active treatment (V4) did not yield significantly lower λ than the three other road verge treatments (V1-3), most likely due to the dry climate and well-drained soils of the studied road verges which provide conditions too xeric for rapid succession (Bennie et al. 2006; Grime et al. 2007). In the long run, however, a time-delayed species extinction may occur ('extinction debt' sensu Tilman et al. 1994) as a delayed response to changes in habitat quality (Eriksson 1996; Helm et al. 2006). This is particularly relevant for long-lived species such as *P. saxifraga*, where longevity significantly enhances species local above-ground persistence (Ozinga et al. 2007) and extends the time lag between habitat deterioration and extinction.

If the repeated cuttings of the present road verge treatment (V1) keep λ under unity, how can the populations exist in the road verges? Several circumstances may explain this paradox. First, only the outermost parts of the road verges (1–2 m closest to the road bed) are twice cut (treatment V1). In wider road verges, the area further in from the road bed receives only a late cut. The moderate effect of litter on seedling establishment in *P. saxifraga* (Hovstad and Ohlson 2008) may allow us to regard the single cutting with hay removal under treatment V3 as representative for this management regime. Moreover, the innermost parts of wide verges (> 3 m) are actually never cut (paralleling treatment V4). Thus, many road verges are subject to mosaic management. Our study shows that some treatments prevent seedling production but increase adult survival (e.g. present treatment V1); others allow seedling production but represent harsher habitats for adult plants (single cutting; V3 and no active treatment; V4). The invasive species *Heracleum mantegazzianum* (Hüls et al. 2007) demonstrated a parallel patterns with high fertility in dense stands (acting as sources of propagules) and high survival and growth in open stands (representing invading fronts for further spread). For *P. saxifraga*, persistent and seedling-producing populations prevail in the inner parts of the road verge, whereas the outer parts (prevented from seedling production by management) receive seeds by dispersal from inner parts of the verge, thereby constituting a fine-grained source-sink situation (Eriksson 1996). Appropriate management of populations in the increasingly fragmented, modern landscape must consider dispersal-related interactions between subpopulations (Runge et al. 2006). A better understanding of potential management-induced metapopulation dynamics in road verges could add both to our general understanding of source-sink dynamics, as well as aid the management of such habitats.

The spatial differentiation of high survival and successful reproduction in road verge population of *P. saxifraga* can partly lift the above-mentioned paradox of $\lambda < 1$ values in stable populations: if we consider that the plants in the different parts of the road verge form one population, the population growth rate of the entire population

might be higher than expected from λ -values of each of the differently managed parts of the population. For road verge population MV we indeed find a lower mean λ of MV1, MV3 and MV4 (0.974, Fig. 2) than the λ -value of a matrix constructed with the means of the vital rates of MV1, MV3 and MV4: 1.000. This important 2.7% increase in λ turns a projected population decline into projected stable population size. Of course, this exercise depends on the proportions of the population subjected to the different management regimes, on the dispersal capacity of seeds, and on spatio-temporal fluctuations in management. Calculations also reveal smaller λ -increase for the other two road verge populations (SV: 0.9% increase from 0.893 to 0.901; NV: 0.4% increase from 0.951 to 0.955). However, it demonstrates clear potential for mosaic management to increase population growth rates in perennial plant species.

4.3 *Spatial variation is larger than the effect of treatments*

Considerable variation between sites (in particular the pastures) modified or even overruled the treatment effects on *P. saxifraga*. Reinstatement of traditional management (P2) in Molde pasture increased λ , as cutting benefited both survival, development into flowering stages and seedling establishment (ω). In the dry Stuvane pasture, low stocking rates due to low production capacity had allowed a thick moss mat to develop, which probably reduced ω and kept λ low under both pasture treatments. Reduced grazing threatens many species in European grasslands (e.g. Poschlod et al. 1998) as trampling livestock is necessary to create microsites for seedling establishment. However, in Nese pasture, high stocking rates combined with reinstatement of cutting (P2) prohibited growth into flowering stage, thereby lowering λ . Increased survival or stasis countered this effect, once more demonstrating a trade off between fecundity and longevity.

A study of the relationship between the vegetation variation and explanatory variables in the sites (Auestad et al. 2008) revealed two main environmental gradients for the *P. saxifraga*-rich vegetation; one related to management, and another related to edaphic conditions (soil moisture and nutrients). Interestingly, the latter separated the three pasture sites with the low- λ Stuvane pasture appearing in the dry and poor end, and the high- λ Molde pasture in the wetter and richer end (Auestad et al. 2008). Hence, environmental variables structuring the vegetation also impacted strongly on the population growth rate, as also demonstrated for the shrub *Purshia subintegra* (Maschinski et al. 2006), and *Scorzonera humilis* (Colling and Matthies 2006). Our study confirms the general relations between demographic performance and environmental factors, and furthermore indicates that environmental conditions may overrule the effect of the present treatments. If the capacity to compensate for removal of reproductive structures is resource limited for polycarpic plants like *P. saxifraga* (as suggested by Huhta et al. 2009), the species may well have tolerated the biomass removal of the various treatments better under resource-rich conditions. The low annual precipitation of the study area (500 mm) probably counteracted potential vegetation overgrowth that could be expected to suppress the low-growing study species in the richest sites.

4.4 *Management implications*

Road verges represented suboptimal habitats for *P. saxifraga* compared to pastures. The present road verge treatment of two cuttings is unfavourable for this late-flowering, perennial herb, as well as for the majority of vulnerable and declining species of semi-natural grassland (Jantunen et al. 2007). Despite their ability to compensate for the

1 biomass loss by higher survival and increased size, few of these species flower early
2 enough to complete their life-cycle under such a regime.

3 However, the linear nature of road verges enables fine scale, zonal application of
4 various management regimes (a ‘mosaic management’ situation). Whether mosaic
5 management may have a parallel effect on other species depends on species’ life history
6 characteristics in combination with specific management regimes. Some examples
7 exists, such as the positive effect of roadwork events on the maintenance of Australian
8 *Acacia* populations (Spooner et al. 2004). Parallel to the pattern observed for *P.*
9 *saxifraga*, mature acacias growing in the innermost, undisturbed parts of the verges
10 produced seeds that germinated in the disturbed, outer parts. Mosaic application of
11 management may also allow species with different habitat preferences to coexist in road
12 verges, i.e., road verges may host both flower-visiting insects that prefer vegetation
13 mown twice a year with hay removal (Noordijk et al. 2009), early-flowering herbs that
14 depend on late mowing to ensure successful seed set (Jantunen et al. 2007) as well as
15 late-flowering species like *P. saxifraga* that actually appears to manage better under
16 abandonment than under repeated mowing. However, for *P. saxifraga* (as for many
17 other perennials) slow dynamics rather than tolerance to overgrowth explain the
18 apparently beneficial effect of abandonment. This particular species may germinate
19 under considerable litter layers, but its’ intolerance of closed canopy may eventually
20 lead to local extinction. To specifically maintain late-flowering, light-demanding
21 grassland species like *P. saxifraga*, we generally recommend road verge management
22 regimes to include at least one annual cutting, avoiding the seed set periods. The
23 positive effect of pasture treatments indicates that cutting in spring and early autumn
24 (parallel to the timing of grazing) may represent beneficial alternatives to summer
25 cuttings, but this remains to be investigated.

26 Despite the obvious effects of management, we found that the local edaphic,
27 climatic and management history related conditions modified or even overruled the
28 effect of management regimes. Demographic studies may, however, pinpoint vulnerable
29 life history components, which in turn may be modified by deliberate actions (e.g.
30 increase stocking rates to increase small-scale disturbance essential for seedling
31 establishment). However, the contradictory effects of management underline Menges’
32 (2000) point that the wide demographic variation between populations necessitates
33 studies of multiple populations. Jongejans and de Kroon (2005) pointed to the danger of
34 using site-for-year substitution in population studies, and we add a caution in
35 transferring management strategies along environmental gradients.

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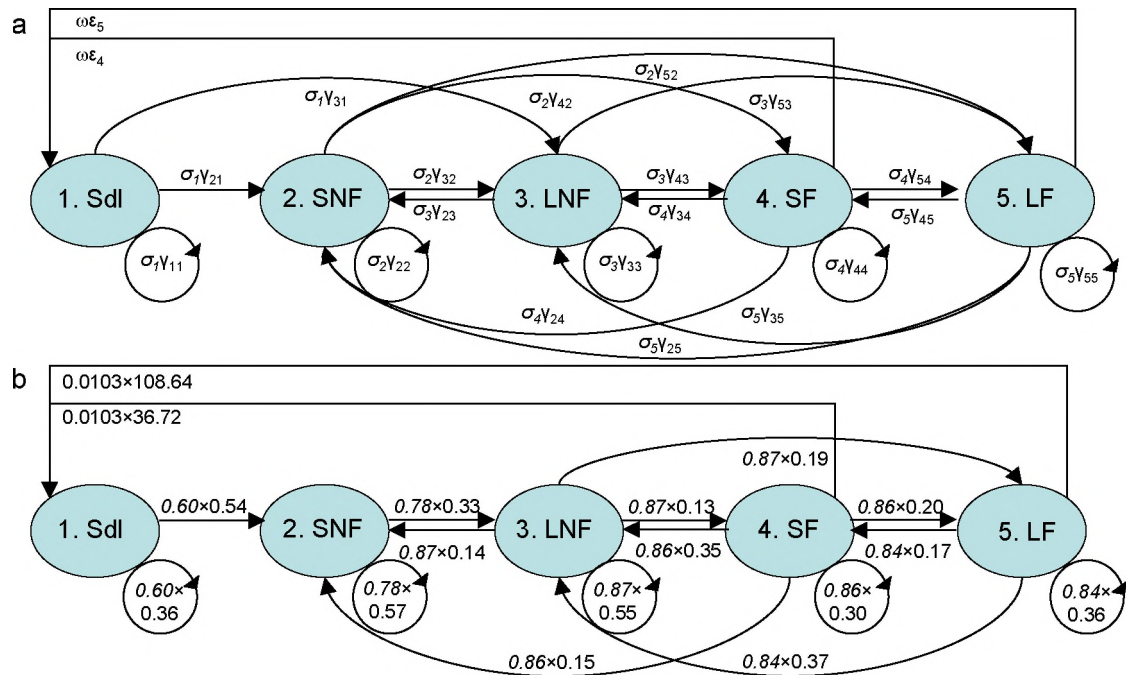


Fig 1 – Five-stage life cycle graph of *Pimpinella saxifraga*. The five stages are 1. Sdl (seedlings), 2. SNF (small non-flowering plants), 3. LNF (large non-flowering plants), 4. SF (small flowering plants) and 5. LF (large flowering plants). (a) Total life cycle graph showing how vital rates combine to yield the corresponding transition values. The vital rates are σ_j (survival); growth ($\gamma_{i>j}$), retrogression ($\gamma_{i<j}$) and stasis ($\gamma_{i=j}$) rates; ε_j (class-specific seed production) and ω (site-specific seedling germination rate averaged over sites). (b) Vital rate values for the average matrix (across all treatments and sites) for transitions > 0.1 , the survival rates in italics. Except for ε_i , all rates are proportions.

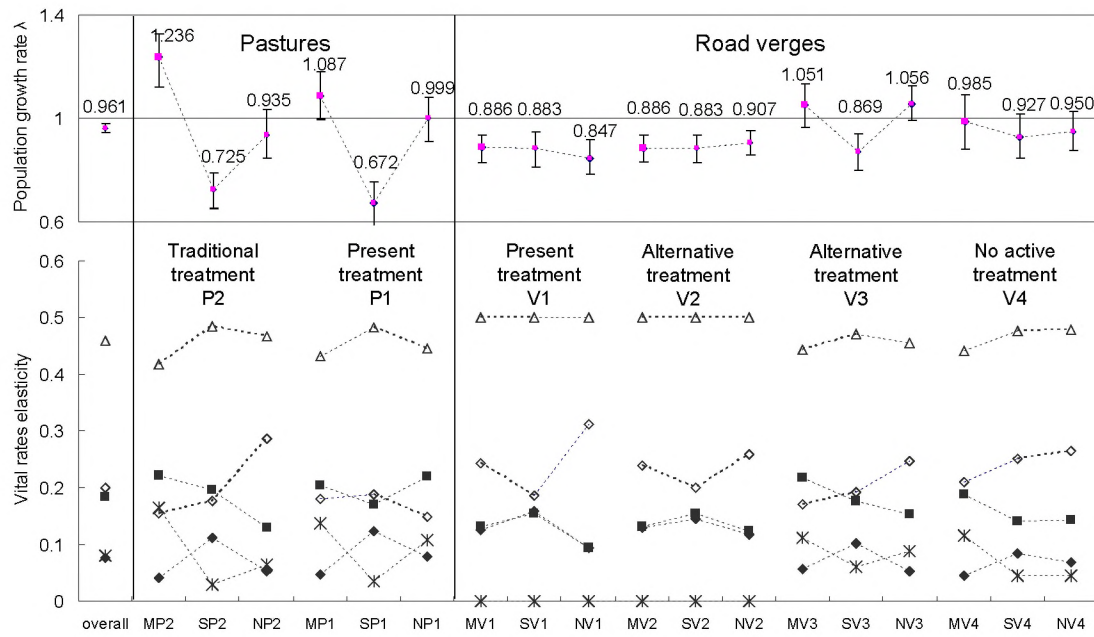


Fig 2 – Population growth rates (λ) and summed elasticity values for vital rates of *Pimpinella saxifraga* in overall and 18 site-treatment populations; four road verge treatments (V1-V4) and two pasture treatments (P1 and P2) in sites Molde (M), Stuvane (S) and Nese (N). Treatment V1: cutting in June and August, no hay removal, V2: like V1 but includes hay removal, V3: August cutting and hay removal and V4: no management. P1: spring and autumn grazing and P2: like P1 plus August cutting with hay removal. Upper panel: λ values with error bars representing 95% CI. Lower panel: Rescaled elasticities of vital rates survival σ_j (Δ), growth $\gamma_{i>j}$ (\diamond), stasis $\gamma_{i=j}$ (\blacksquare), retrogression $\gamma_{i<j}$ (\blacklozenge) and fertility ε_j and ω (\times) for all site-treatment combinations.

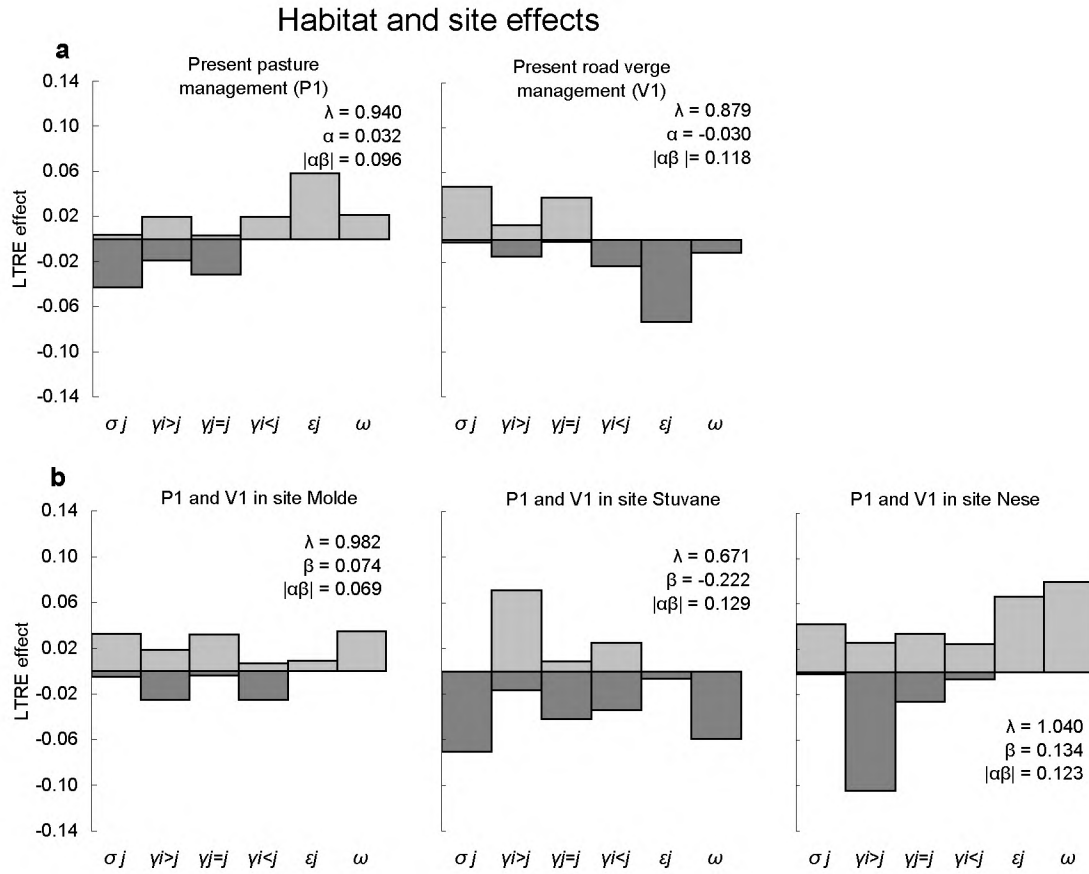


Fig. 3 – LTRE-effects of habitat (present treatment in road verges; V1 and pastures; P1) and site, evaluated against their mean matrix ($\lambda = 0.908$). Positive and negative contributions are grouped by vital rate, symbols as in Fig. 1. (a) Overall effect of habitat V1 and P1. (b) Effect of site (Molde, Stuvane and Nese), averaged across habitats (P1 and V1). Mean λ , habitat effect α or site effect β and mean absolute interaction effect ($|\alpha\beta|$) are given. See Appendix E (Table E1) for LTRE contributions.

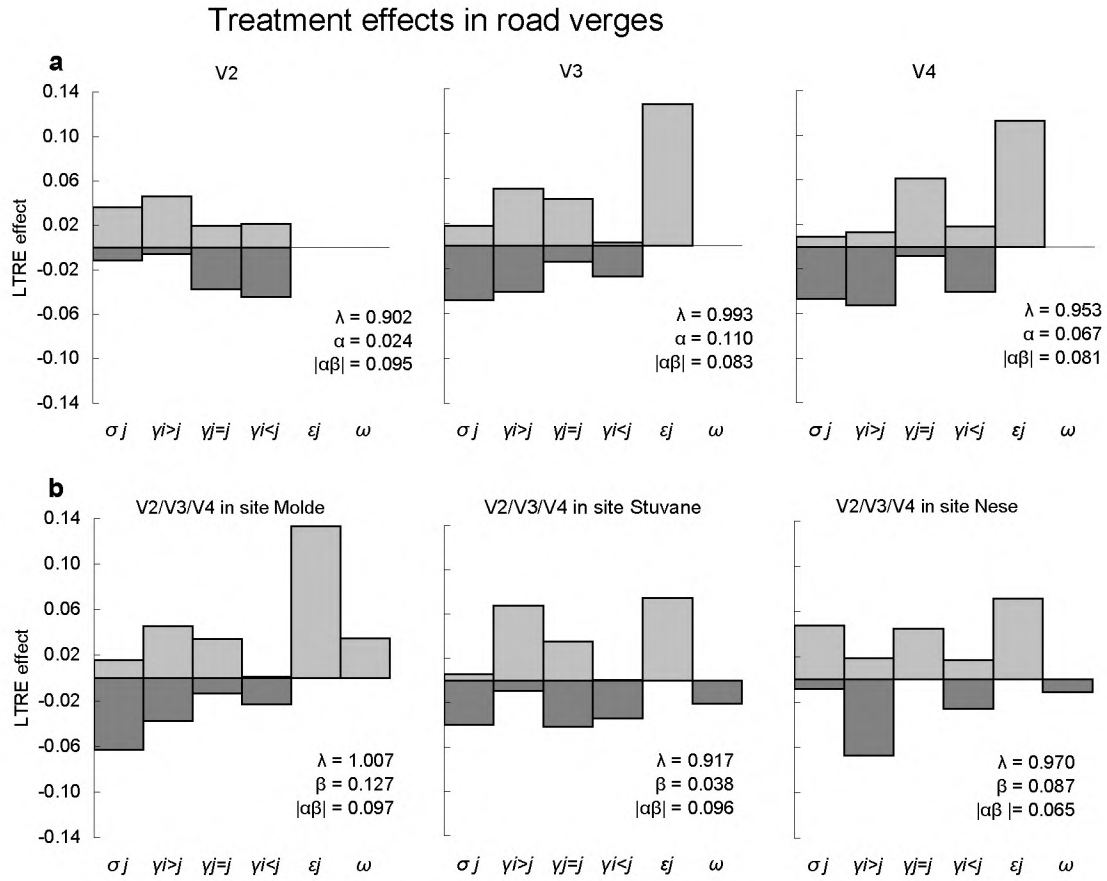


Fig. 4 – LTRE-effects of alternative road verge treatments (V2, V3 and V4) and site, evaluated against V1 ($\lambda = 0.879$). Positive and negative contributions are grouped by vital rate, symbols as in Fig.1. (a) Effect of treatments (V2, V3 and V4) averaged over sites. (b) Effect of site (Molde, Stuvane and Nese), averaged over treatments V2, V3 and V4. Mean λ , treatment effect α or site effect β and mean absolute interaction effect ($|\alpha\beta|$) are given. See Appendix E (Table 2) for LTRE contributions.

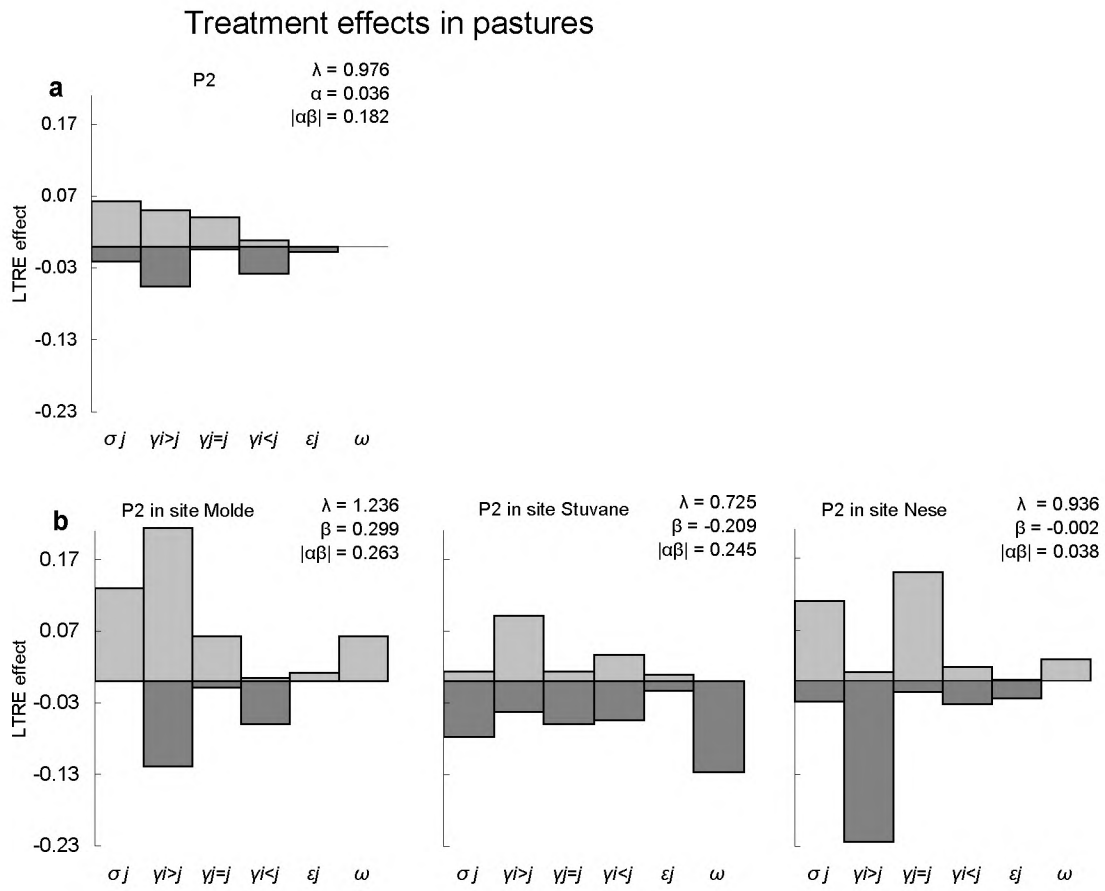


Fig. 5 – LTRE-effects of traditional pasture treatment (P2) and site, evaluated against present pasture treatment P1 ($\lambda = 0.940$). Positive and negative contributions are grouped by vital rate, symbols as in Fig. 1. (a) Effect of P2 averaged over sites. (b) Effect of site (Molde, Stuvane and Nese), averaged over treatment P2. Mean λ , treatment effect α or site effect β and mean absolute interaction effect ($|\alpha\beta|$) are given. See Appendix E (Table 3) for LTRE contributions.

Appendix A-E. Supplementary material

Appendix A. Modelling of dry mass and seed production from morphological measurements

Appendix B. Calculations of the fertility vital rates ω and ϵ_j

Appendix C. Vital rates values for overall and site-treatment matrices

Appendix D. Vital rates values for averaged matrices

Appendix E. LTRE values

Table E1. LTRE values for the comparison of road verges and pastures

Table E2. LTRE values for the alternative road verge management

Table E3. LTRE values for the alternative pasture management